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things about the natural history of the islands which coincide in detail with my own observations.

Professor Chas. F. Holder, an authority on the natural history and ethnology of the California coast islands, believes the quail to be native on Catalina Island. He assures me (in a letter dated April 8, 1906) of their constant abundance there from the time of his first acquaintance with the island 21 years ago.

Therefore the characters of *Lophortyx catalinensis*, as here pointed out, appear to be significant of long isolation, rather than of acquisition within a few years.

Pasadena, California.

ISOLATION VERSUS NATURAL SELECTION.

BY LEONHARD STEJNEGER.

In a recent paper in 'The Auk' (XXIII, April, 1906, pp. 161–171) Mr. Hubert O. Jenkins has given a very instructive account of the 'Variation in the Hairy Woodpecker (*Dryobates villosus* and subspecies)', accompanied (p. 163) by a map of the geographical distribution of the various subspecies recognized by him.

In looking at the map I was forcibly struck by the fact that the boundaries of the various forms do not coincide with those of the various 'life zones' commonly recognized by North American zoölogists. The nearest approach to such a coincidence is the range of *Dryobates villosus leucomelas* and the so-called boreal zone. In the United States the other subspecies show a certain agreement with the two main east and west divisions of the transcontinental belts, the humid and the arid divisions of the transition, upper austral and lower austral life zones. It is a curious fact, however, that while the zoölogists do not recognize an east and west division of the boreal belt, the distribution of the woodpeckers in question clearly indicates that the Pacific slope of the continent included in the boreal zone has some forms as markedly separated from the eastern forms as those further south.

Apparently then temperature, as indicative of the life zones, has very little to do with the distribution and differentiation of these races of woodpeckers. On the other hand, the transverse lines which Mr. Jenkins has drawn on his map "separating forms of equal size" in showing a gradual increase of size northward point to thermal influences, although they do not present any special agreement with the lines on the zonal maps.

Nor do the east and west forms find a ready explanation in the humidity or aridity of the climate, as the western form *D. v. harrisi*, which enjoys a climate fully as humid as typical *D. villosus* in the northeastern United States, is the one most removed from it in color characters. It is true that the western forms to some extent correspond to the humid and arid districts of the Pacific slope in as much as the dark underside of the large northwestern *D. v. harrisi* in a general way coincides with the extent of an annual rainfall of over 50 inches. It is also true, that the range of the small southeastern *D. v. auduboni* falls inside the area in the east having a rainfall of over 50 inches, but the latter amount of precipitation is also found over larger areas inhabited by typical *D. villosus*.

As we go south into Mexico and Central America we meet an increasing darkening of the underside through *D. v. intermedius* to *D. v. jardinii*. This darkening is plainly connected with the increasing amount of the annual precipitation which exceeds 50 inches considerably.

We can thus, in a general way, trace the influence of present climatic conditions in the formation of some of these races, in as much as those distinguished by a darkened underside inhabit districts having a yearly rainfall of 50 inches or more. Present temperature conditions apparently play a very subordinate rôle, except that the size of the various forms gradually increases from the warmer to the colder regions, but apart from the fact that this increase in size can only be very indirectly caused by the temperature, the difference in size is not diagnostic of the various forms, that is to say, the northern individuals of each form are larger than the southern ones (see Jenkin's table on p. 171, showing an average greater size of *D. v. hyloscopus* north of 35° N. lat. than south of it), so that the gradual increase in size northward is a gradual increase in the size of the individuals and thus only indirectly of the races.

It is plain then, that of the present climatic factors determining the formation and the distribution of the forms of *D. villosus*, the rainfall is by far more important than the temperature.

If we examine Mr. Jenkins's map further we discover a doubly curved, solid black line running from N. W. to S. E. "separating heavily and lightly spotted forms." East and north of this line we find forms which have the wing feathers spotted with white to the tips, while the races living west and south of the line have these feathers only spotted at the base. Intermediate specimens are found occasionally along this line.

Mr. Jenkins has tried to explain the variations in these birds "through natural selection and the survival of those best fitted to escape from enemies or to obtain food in the particular region that they inhabit," but he does not seem to have much faith in the explanation. As for the spotting, he reasons that the spots "were originally developed for some good service, as for directive markings, etc." The loss of them at the tip he then suggests as due to the protection it would be to the bird to have the folded wings uniformly black so as "to make the bird less conspicuous while climbing up dark colored tree trunks." But he brings down the whole construction very effectively with the following remark:

"Could this theory be absolutely proven we would still have to explain why all of the Hairy Woodpeckers have not developed in like manner. If we draw a geographical line between light and heavily spotted forms this line would in part coincide with the geographical line between the Arid West and Humid East. But I greatly doubt if aridity and humidity have anything to do with the wing spotting.[1] We might say that the more highly developed form has had more enemies and more competition, but such a statement needs yet to be proven."

Mr. Jenkins in offering his explanation labors under one fundamentally erroneous notion, viz., "that the western bird is more highly developed" (p. 169). He speaks also of "the spots on the inner webs and proximal ends of the feathers" as "more persistent." Evidently he regards the eastern forms with the wings spotted to the

[1] He might have added that plainly it has not in this case, since *D. v. harrisi*, which inhabits the most humid region, is also one of the least spotted forms.—L. S.

tip as the original forms, from which the western birds were derived by a reduction of the spots on the distal end of the wing feathers. Just the opposite is the case.

Speaking of the birds in general it may be said that there is an evolutionary tendency towards a uniformly colored plumage as distinct from the dark-and-light (not black-and-white) spotted or striped plumage. This accomplished, the further development tends towards pure white, either as a uniform white plumage or one spotted with pure white. The white spots are not produced by any white coloring matter, on the contrary, they are due to total absence of pigment. Generally speaking they are a degradational development, they betray a structural weakening of the feather. As for the wing feathers this process usually begins at the base of the feathers, a basal white spot being present in many birds although absolutely hidden. A further development of it is the white wing 'speculum' of so many birds. Often it develops still further, but seldom extends to the very tip, unless the whole plumage tends to uniform white, and it is mostly confined to the part of the feather covered by the superposed portion of the next feather. Where the distally increasing whitening of the feather — and we are now coming to the case of the spotted-winged Woodpeckers — does not proceed as a solid white area, but as a series of white spots, the remaining black cross bars have the function of stays or braces. It is easy to understand then why the white spots appear first on the inner webs of the secondaries and last on the outer webs of the primaries or at the tips which extend beyond the plane of the wing when spread for flight.

That this degradation of the feathers in the birds of northern affinities as a rule increases towards the colder regions there can be no doubt, and as for the spotted woodpeckers of the genus *Dryobates* I need only refer to the Siberian and Kamchatkan forms for proof. That this increase in the size and number of white areas is not *directly* attributable to the effect of the cold seems evident (see my Ornith. Res. Expl. Kamtch., 1885, pp. 343–344). Barrett-Hamilton, not long ago, has suggested a theory connecting the absence of pigment with the accumulation of fat in the underlying tissues of the body, but in the woodpeckers at least I fancy it would be difficult to establish such a connection. It seems to me,

however, that perhaps ease of living combined with the cold climate of the North and may be some other less important or more obscure conditions, may account for the phenomenon. It must not be imagined that because the northern birds live in a cold climate they have a particularly hard life. Food is very abundant there, perhaps more so than in the southern latitudes, and the large size of these northern birds may be thus accounted for by the combination of plentiful food and vigorous, energetic exercise necessitated by the cold.

That there is some connection between the more or less heavy spotting and the north-south distribution is very probable. The coincidence of these facts among a large number of species of woodpeckers, especially in Japan, shows this clearly. Let us take a single example from the closely allied genus *Yyngipicus*. Beginning in the Riukiu archipelago with the small dark *Y. nigrescens*, we find, as we go northwards, *Y. kizuki* in Kiusiu and Hondo and finally in Yezo the largest and most spotted of them *Y. seebohmi*, a regular gradation from south to north.

How are we then to explain that the increase of spotting in North America is essentially west-east and not a south-north phenomenon?

We have seen that the present climatic conditions give no clew, but perhaps we may find it in the 'environmental stress' of a previous geological period.

The relation of our spotted woodpeckers to the Old World species of *Dryobates* and the geographic distribution of the latter is such that we must conclude that ours arrived to this continent from eastern Asia, and various considerations make it probable that this immigration took place not later than Pliocene times. We may then assume that previous to the Glacial period there lived in North America a Hairy Woodpecker small of size. The southern specimens probably resembled *D. v. jardinii*, the northern ones were possibly more like *D. v. auduboni*. The advance of the glaciation pushed the woodpeckers southward and in combination with the transgression of the Gulf of Mexico affected a separation of the southern Alleghany region from the western portion of our continent which then as now formed the northern continuation of Mexico. It is well within the bounds of probability that the Hairy Woodpecker which became isolated in the Alleghanian region

belonged essentially to the form which above I have compared to *D. v. auduboni*, and that on the other hand, the one which was forced south in the Sonoran region mostly consisted of scantily spotted southern specimens comparable to *D. v. jardinii*. I feel convinced of the correctness of the hypothesis that it was during this long period of separation that the two main forms, the western and the eastern, finally got established. I am even strongly inclined to believe that by the time of the last retreat of the glacial covering the two forms were so well differentiated that they might be called species rather than subspecies, as these terms are now commonly used. The two now distinct species of Hairy Woodpeckers following the melting ice cap and occupying the forests which gradually covered the reclaimed land finally met along the solid line of Mr. Jenkins's map, assuming a distribution such as we see it at the present day. That the two species which were established through some such separation should intermingle to a considerable extent along their mutual boundary line is quite natural. I leave it to those ornithologists who are more familiar with the forms in question to decide whether the 'intermediate' specimens, where the eastern and western birds come into contact, may not properly be regarded as the result of hybridization. The formation of the three eastern and four western races, chiefly characterized by size, amount of darking of the underside and extent of the white spots, is then subsequent to the primary segregation of the eastern and western species. There is nothing in the quantity or quality of their specialization which contradicts the assumption that they were formed since the glacial period.

The above seems to me to be a much more satisfactory theory as to the origin of the various forms of the Hairy Woodpecker, than the one suggested by Mr. Jenkins. That natural selection at some stage or another in the evolution of these forms, may have exercised an auxiliary influence it is not necessary to deny, but I think there can be but little doubt that 'environmental stress' working on a material possessing considerable plasticity in a certain direction accomplished the 'speciation' of these forms because of their complete *isolation* during an earlier geological period.